A Stochastic Stage-Based Population Model of the Sandbar Shark in the Western North Atlantic

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Abstract.—The sandbar shark *Carcharhinus plumbeus* is the most important species caught in the commercial shark fishery operating off the U.S. Atlantic and Gulf of Mexico coasts. Previous demographic studies of this and other species of sharks have utilized age-structured, deterministic life tables that provided point estimates of maximum rates of increase. To reduce some of the uncertainty in estimates of age at maturity and longevity—especially acute in the case of the sandbar shark—I constructed a stage-based model based on an Usher matrix that utilizes the more reliable estimates of size at maturity and maximum size for this species in the northwest Atlantic. Because demographic variability also can affect estimated rates of increase, I introduced stochasticity into the model by randomly selecting fecundity rates from an empirically determined distribution, and natural mortality rates from estimates obtained through four life history methods. The simulation model was applied to females only. Population projections 20 years forward in time without exploitation predicted slowly growing populations at approximately 1.3%/year. Application of a constant instantaneous mortality rate (F) of 0.1 to each stage-class separately indicated that removal of large juveniles would produce the greatest population declines, whereas removal of age-0 individuals would be sustainable. The simulation model was then used to predict potential outcomes under three hypothetical harvesting scenarios using the current U.S. commercial quota indicating that all strategies produced pronounced population declines.

In general, population dynamics are governed by ecological and genetic processes. From an ecological perspective, vital rates are influenced by demographic and ecological processes and diverse sources of stochasticity which ultimately determine the growth or decline of a population (Figure 1). In sharks, knowledge of vital rates is fragmentary at best due to the lack of basic biological information. Furthermore, knowledge of dispersal rates, spatial composition of populations, stock–recruitment dynamics, and the effect of environmental stochasticity on populations is practically nonexistent. This paucity of scientific information has prompted the emergence of life tables, which require comparatively little data to describe shark populations (see Cortés, 1998).

The main value and drawback of life tables lies in their simplicity. Life tables provide "snapshots" of populations, in contrast to other more comprehensive models, which may capture the spatiotemporal stock dynamics. However, more comprehensive models require more detailed information that generally will not be available for sharks, and thus have the risk of giving the illusion of exactitude when in fact the modeling may be based on poor or insufficient data (Burgman et al. 1993). The Leslie matrix approach (Leslie 1945) is a good compromise between life tables and other more detailed fishery models and provides a framework for incorporating density-dependent (nonlinear) and stochastic changes in age-structured populations (Getz and Haight 1989). Owing to the uncertainties associated with estimates of age at maturity and longevity in sharks, use of stage-based matrices (Lefkovitch 1965; Usher 1966; 1969) analogous to the age-based Leslie matrix may be preferable because the stage-based approach can take advantage of size information, such as size at maturity and maximum size, which is easier to obtain in sharks.

Vital rates vary over time (Caswell 1989). However, matrix population models describe the current demography and project it infinitely into the future by assuming that the projection ma-
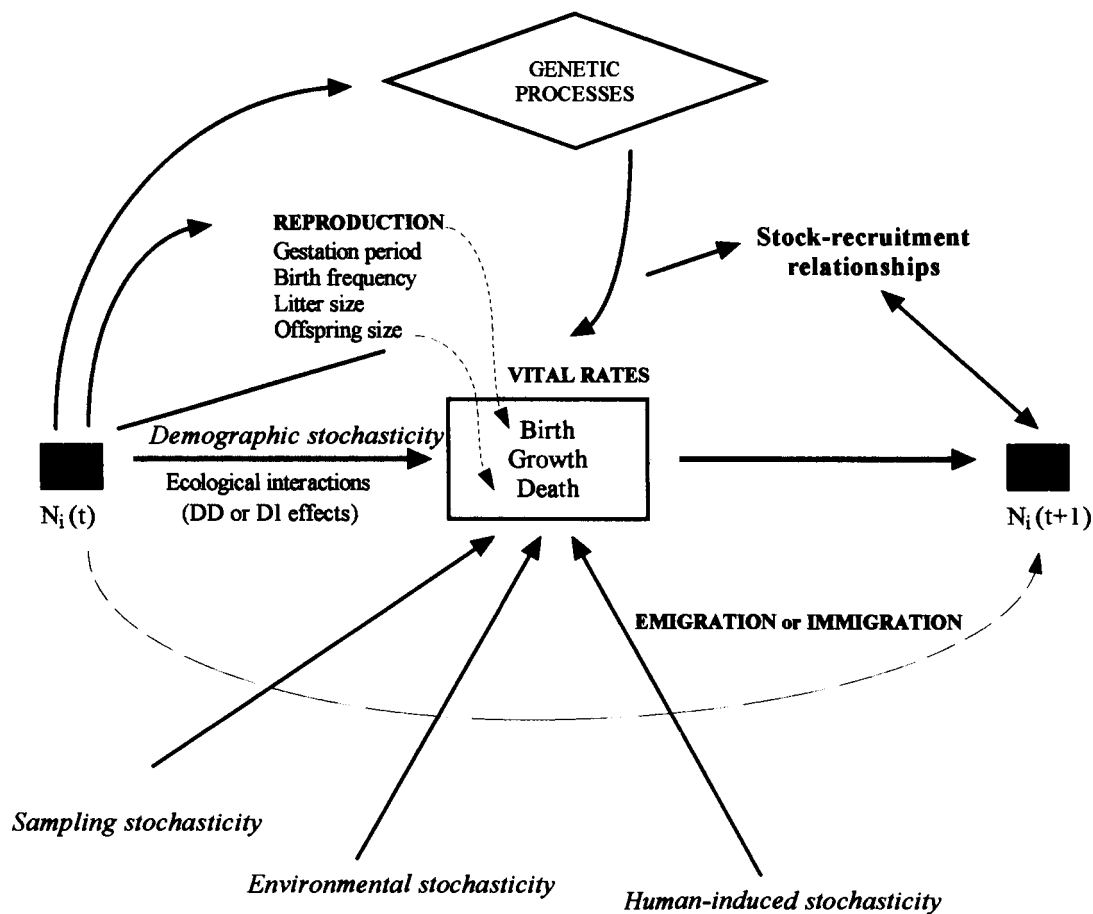
FIGURE 1.—Diagram of the ecological and genetic processes affecting population dynamics in sharks. Population size at time t and $t + 1$ is shown as a solid rectangle. Modified after Schemske et al. (1994).

trix and vital rates associated with it do not vary over time. This deterministic approach does not contemplate the variation and uncertainty associated with demographic schedules that are likely to affect populations in the short term and can thus be misleading for population projections (Burgman et al. 1993). A more realistic approach is to introduce stochastic demographic fluctuation by varying vital rates over time, as opposed to fixing them. This probabilistic framework allows assessment of risks associated with both natural variability and exploitation.

The objective of this paper is to generate population growth rates for the sandbar shark without the limitations imposed by deterministic and asymptotic methods and our limited knowledge of age at maturity and longevity for this species. First, I use a stage-structured model based on an Usher matrix to introduce demographic stochasticity into the model by varying birth and natural mortality rates and project population abundance through Monte Carlo simulations twenty years forward in time. Second, I repeat the simulations of population trajectories, but apply a constant, moderate removal rate to each of the stage-classes separately. Third, I use the model to predict future population sizes under three hypothetical harvesting scenarios based on a constant quota: (1) removal of neonate, young-of-the-year, and small juvenile individuals, (2) removal of large juveniles and subadults, and (3) removal of adult individuals. Finally, I compare the results with predictions from published life table studies for this species.

Methods

Demographic Parameters

Size-specific annual natality for sandbar sharks was calculated from data presented in Sminkey and Musick (1995, 1996). Aspects of fecundity considered to calculate reproductive output included the mean number of pups per female (mean = 8.4 ± 2.3 SD), the periodicity of parturition (biennial), the sex ratio of offspring at birth (very close to 1:1), and the percentage of mature females at size (25% of females 168–179 cm total length [TL] mature; 100% of females > 180 cm TL mature). Additionally, it was assumed that all mature females were reproductively active in any given year.

Survivorship was calculated from estimates of mortality obtained through four life history methods: (1) an equation by Hoenig (1983) relating longevity to total instantaneous mortality rate (Z), (2) an equation by Pauly (1980) that relates instantaneous natural mortality rate (M) to von Bertalanffy growth function (VBGF) parameters and an estimate of the mean annual water temperature where the population occurs, (3) a method by Chen and Watanabe (1989) that also relates M to VBGF parameters, and (4) an equation by Peterson and Wroblewski (1984) that relates M to body weight. Methods (1) and (2) have been described elsewhere (Cortés and Parsons 1996; Cortés 1998); methods (3) and (4) are described extensively in Roff (1992) and allow estimation of age- and size-selective natural mortality, respectively. Chen and Watanabe's method generates two functions: one that predicts age-specific estimates of M for early and middle life phases, and one that produces an average M estimate for senescent phases. Peterson and Wroblewski's method (1984) relating size to M was originally developed for pelagic fish, but was shown to predict well mortality rates over 16 orders of magnitude (McGurk 1986). The equation is:

$$M = 1.92\ W^{-0.25}$$

where M is natural mortality rate per yr and W is weight in g. Weight for the sandbar shark was obtained from length through the equation (Kohler et al. 1995):

$$W = 0.0000109\ FL^{3.0124}$$

where W is weight in kg and FL is fork length in cm.

For this analysis I classified sandbar sharks into six stages: (1) neonates and young of the year, (2) small juveniles, (3) large juveniles, (4) subadults, (5) young adults, and (6) large adults (Figure 2 and Table 1).

The Stage-Structured Model

The current population dynamics of the sandbar shark were modeled by using a stage-structured matrix approach (Lefkovitch 1965; Usher 1966, 1969; Caswell 1989; Getz and Haight 1989) implemented on commercially available spreadsheet software. The model can be expressed in general terms as:

$$\mathbf{x}\,(\,t+1\,) = \mathbf{Ax}\,(t)$$

where $\mathbf{A}$ is an $n \times n$ transition matrix and $\mathbf{x}$ is a vector representing the population size structure. Solutions to the above model are typically obtained from the general matrix model:

$$\mathbf{Ax} = \lambda\mathbf{x}$$

where λ is the set of eigenvalues of $\mathbf{A}$ corresponding to the eigenvector $\mathbf{x}$. In traditional analyses, the population will grow toward a stable stage distribution in multiples of λ_Δ (the dominant eigenvalue) as determined by the relative size of the elements of the eigenvector corresponding to the dominant eigenvalue (Getz and Haight 1989). Note that $\lambda = e^r$, where r is the intrinsic rate of increase.

In contrast to the Leslie model for age-structured populations (Leslie 1945), which assumes that all surviving individuals in a given age-class move up to the next age-class in one time period (year), the stage-structured model considers two components: the proportion of individuals in a given stage-class i at time t that move on to the next stage-class at time $t+1$ (G_i) and the proportion of individuals in stage-class i that remain behind (P_i) (Figure 2).

As described by Crouse et al. (1987) and Caswell (1989), the transition probabilities G_i and P_i can be estimated from the stage-specific survival probabilities p_i and the stage duration d_i. Size-specific survival probabilities were calculated through the life history methods described in the previous section after transforming ages into lengths through the VBGF derived by Sminkey and Musick (1995), and lengths into weights through the length-weight relationship described above (Kohler et al. 1995) when appropriate.

Proportions G_i and P_i were calculated as described in Crouse et al. (1987) and Caswell (1989), such that:
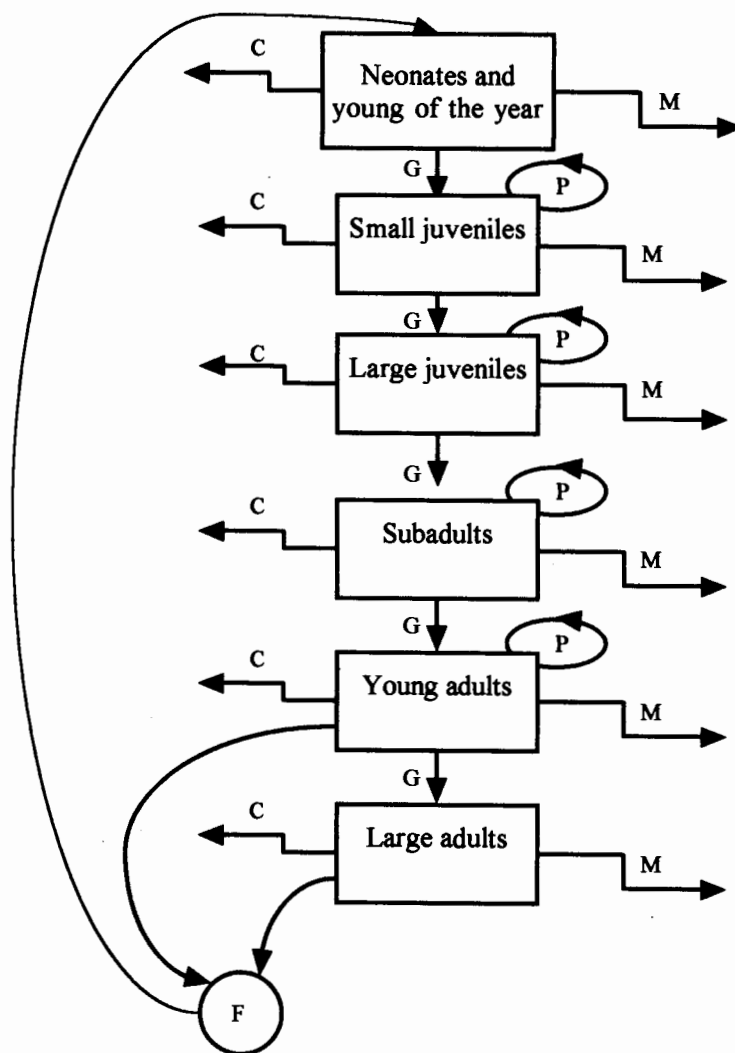
FIGURE 2.—Schematic representation of the life cycle of sandbar sharks, including the stages (boxes) considered in this study, transition probabilities between stages (P is the probability of remaining in the same stage and G is the probability of moving to the next stage), losses to the population due to natural mortality (M) and catches (C), and gains to the population due to reproductive output (F).

TABLE 1.—Stages for sandbar sharks in the northwest Atlantic Ocean.

Stage-class (number)	Size (cm total length)	Mean weight (kg)	Approximate ages (yr)	Stage duration (d_i; yr)
Neonates and young of the year (1)	60–74	1.7	0	1
Small juveniles (2)	75–107	5	1–3	3
Large juveniles (3)	108–153	15	4–9	6
Subadults (4)	154–168	27	10–12	3
Young adults (5)	169–189	38	13–18	6
Large adults (6)	190–233	56	19–35	17

$$G_i = \frac{p_i^{\,d_i}(1 - p_i)}{1 - p_i^{\,d_i}}$$

and

$$P_i = \left(\frac{1 - p_i^{\,d_i - 1}}{1 - p_i^{\,d_i}}\right) p_i$$

where, in the present study, p_i is the mean of the age-specific survivorship values S_j from S_1 to S_{d_i}, S_j is survival from age j to age $j + 1$, $S = e^{-z}$, and d_j is stage duration in yr. In addition, the proportion of individuals alive in the first cohort, or p_0, was set to 1.

Recruitment of newborn sharks (x_0) was considered a linear function of maternal stock size, such that:

$$x_0(t + 1) = \sum_{i=1}^{n} b_i x_i (t + 1)$$

where b_i is the number of female offspring per female at stage i and n is the number of stages (6).

Population Projections

Monte Carlo simulations were used to reflect the uncertainty in the estimates of natural mortality and the variability in fecundity among individuals. Sminkey and Musick (1996) found a positive relationship between maternal size and litter size, but the correlation was weak and there were not enough litters at size to calculate size-specific distributions of fecundity. Hence, size-specific fecundity was randomly selected from a single normal distribution with mean = 8.4 and SD = 2.3. Size-specific estimates of natural mortality for neonate and young-of-the-year sandbar sharks, small and large juveniles, and subadults up to age 11 (the age in method (3) after which M is considered constant and the second function applies) were randomly selected from a pool containing the pairs of values generated through life history methods (3) and (4) described previously; size-specific estimates of M for age-12 subadults and young and large adults were randomly chosen from a pool containing the four values generated through the four life history methods. All estimates of M were given equal probabilities.

A vector x representing the population size structure was generated from a life table presented in Cortés (1998) assuming an almost stationary population $(r = 0.003)$ and an arbitrary initial population abundance of 1,000,000. Starting with this initial stable stage distribution at time 0, population trajectories were projected 20 years into the future by allowing estimates of vital rates to vary randomly from year to year. This process was repeated 100 times and a set of histograms of the relative change in population size after 5, 10, 15, and 20 years was generated with the 100 trajectories obtained. Note that model projections are unaffected by the choice of initial population abundance.

The effect of commercial harvesting also was evaluated within the framework of the stage-structured model, so that:

$$x(t + 1) = Ax(t) - u(t)$$

and

$$u = HAx$$

where u is an exploitation vector representing the number of individuals removed from the ith stage-class, and H is a diagonal matrix with ith diagonal element h_i, the proportion of individuals removed from the ith stage-class.

A constant instantaneous fishing mortality rate (F) of 0.1, equivalent to a removal rate of approximately 10% $(e^{-F} = 0.905)$, was applied separately to each stage-class to examine the behavior of the populations in each case.

The current U.S. annual commercial quota for large coastal sharks in the northwest Atlantic (1,285 metric tons) also was applied, based on the following assumptions: a conversion factor of 1.39 was used to transform landed to whole weight (FDEP 1996), sandbar sharks make up approximately 60% of the total combined landings, and sex ratios of landings are close to 1:1 (Branstetter 1996). Three harvesting strategies were explored, each of which removed 535,845 kg, respectively, of (1) neonates, young of the year, and small juveniles, (2) large juveniles and subadults, and (3) young and large adults. For each strategy 50% of the quota was applied to females only of each of the two stages considered. Thus, for strategy (1) 267,922.5 kg, equivalent to 157,601 neonate and young-of-the-year individuals assuming a mean weight of 1.7 kg (Table 1), or 61.6% of the initial abundance in that stage, were removed. Likewise, 267,922.5 kg, equivalent to 53,585 small juveniles assuming a mean weight of 5.0 kg (Table 1), or 19.8% of the initial abundance in that stage, also were removed. The same rationale was used for strategies (2) and (3), which was equivalent to removing 7.1% of all large juveniles and 13.9% of all subadults in strategy (2), and 8.4% of all young adults and 7.0% of all large adults in strategy (3).

In both cases (application of $F = 0.1$ and quota), the simulations were started assuming an initial stable stage distribution at time 0. Population trajectories were projected 20 years forward in time by allowing estimates of vital rates to vary randomly from year to year but keeping removal rates constant from year to year. This process was repeated 100 times for each fishing strategy and a set of histograms of the relative change in population size after 5, 10, 15, and 20 years was generated with the 100 trajectories obtained and the probabilities of different levels of population increase or decline quantified.

Results

Annual survivorship values (S) calculated through the four life history methods were remarkably consistent (Figure 3). Hoenig's method yielded a value of 0.891 for a longevity of 35 years and Pauly's method produced a value of 0.839. Survivorship calculated through Chen and Watanabe's equation ranged from 0.739 to 0.888 for ages 0–11, and was 0.907 for sharks age 12 or older (Figure 3); Peterson and Wroblewski's method yielded values that ranged from 0.742 for neonates to 0.886 for the largest adults.

The initial stable stage distribution constructed after the life table by Cortés (1998) was dominated by three stages: neonate and young-of-the-year, small juvenile, and large juvenile sandbar sharks, in similar proportions (about 25% each; Table 2). Subadults and young and large adults made up the remaining portion (25%) of the population.

TABLE 2.—Stable stage distribution for sandbar sharks calculated after a life table by Cortés (1998).

Stage-class (number)	Stable stage distribution
Neonates and young of the year (1)	25.6%
Small juveniles (2)	27.1%
Large juveniles (3)	25.0%
Subadults (4)	7.1%
Young adults (5)	8.4%
Large adults (6)	6.8%

Mean projected population abundance, calculated as the proportional change in population size from one year to the next, steadily increased at an average rate of about 1.3%/year over the 20-year period considered when no exploitation took place (Figure 4). Mean population size increased by 13.6% (95% confidence interval (CI):13.2%–14.1%), 17.2% (16.7%–17.8%), 22.4% (21.9%–23.0%), and 28.3% (27.6%–28.9%) after 5, 10, 15, and 20 years, respectively (Figure 4 and Appendix Figure 1).

The simulations including $F = 0.1$ at each stage-class revealed that large juveniles were the most vulnerable stage, followed by young and large adults, whereas neonate and young-of-the-year sandbar sharks were the least susceptible under this strategy (Figure 4 and Appendix Figure 1). Removal of neonate and young-of-the-year sharks at this level of F still allows for population abundance to slowly increase, such that after 20 years mean population size would increase by 13.3% (12.7%–13.9%; Figure 4 and Appendix Figure 1) at an average rate of about 0.6%/
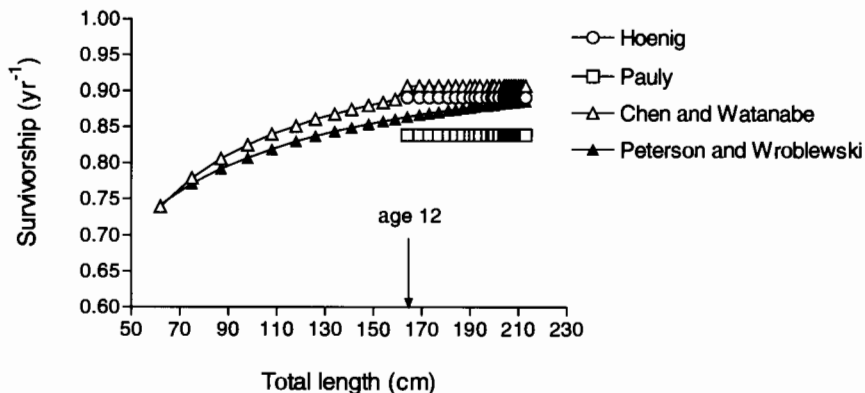

FIGURE 3.—Natural mortality estimates, expressed as annual survivorship, for the sandbar shark using four life history methods. Starting at age 12, Chen and Watanabe's method predicts a constant value of natural mortality. See text for a description of the methods.
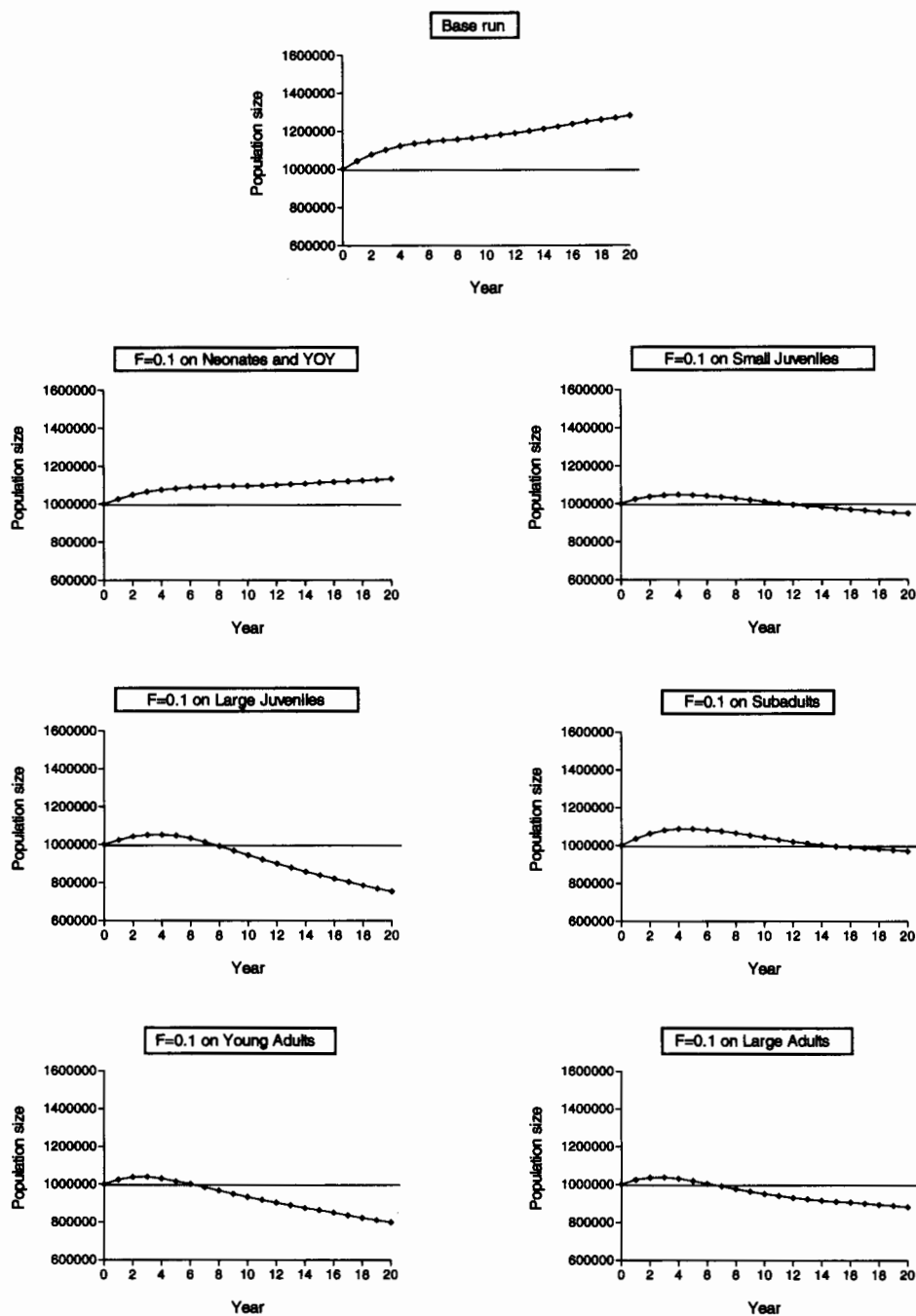
FIGURE 4.—Mean trajectories simulating the future abundance of an undisturbed population (base run) of sandbar sharks in the northwest Atlantic over a 20-year period and when subjecting stage 1 (neonate and young-of-the-year), stage 2 (small juvenile), stage 3 (large juvenile), stage 4 (subadult), stage 5 (young adult), and stage 6 (large adult) individuals, respectively, to a removal rate of $F = 0.1$. Each curve is the mean of 100 realizations, each of which started at Year 0 with a stable stage distribution of 1,000,000 females. Abundance at each subsequent time step was determined by randomly choosing birth and death rates from statistical distributions.

year. Under the same regime, removal of small juveniles results in slowly declining population abundance after 5 years to a mean of −5.2% (−5.9% − −4.6%) after 20 years (Figure 4 and Appendix Figure 1). Removal of large juveniles results in the greatest population declines, peaking at −24.6% (−25.0% − −24.1%) after 20 years (Figure 4 and Appendix Figure 1). Subadults were the second-least susceptible stage, yet mean population abundance decreased below the initial value of 1,000,000 individuals after 15 years reaching −3% (−3.6% − −2.5%) after 20 years (Figure 4 and Appendix Figure 1). Mean population trajectories for young adults and large adults were very similar up to year 6, at which point they had decreased roughly to the initial level of abundance, but after that point mean population decrease for young adults was increasingly more accentuated than for large adults until reaching a low of −20% (−20.4% − −19.5%) after 20 years (Figure 4 and Appendix Figure 1).

Application of the present U.S. commercial quota under the three harvesting scenarios produced declining populations after 20 years in all cases. Removal of neonate, young-of-the-year, and juvenile individuals (strategy 1) produced a precipitous decline in population abundance, such that after only 5 years it had been reduced to about 67.1% (66.8%–67.5%) of its initial value (Figure 5 and Appendix Figure 2). Removal of large juveniles and subadults did not yield relative declines until after 5 years, but mean population abundance had been reduced by −41% (−41.3% − −40.7%) at the end of the simulation period (Figure 5 and Appendix Figure 2). Similarly, removal of young and large adults resulted in a mean decline in population abundance of −37.9% (−38.3% − −37.5%) after 20 years (Figure 5 and Appendix Figure 2).

Discussion

The simulations indicate that undisturbed populations could slowly increase at an average rate of about 1.3% per year over the 20-year projection period. This result is not dissimilar to intrinsic rates of population increase (r) calculated with deterministic, static life tables by other authors (Table 3). However, use of r or the finite rate of population increase (e^r) or dominant eigenvalue (λ) as predictors of future population growth can be misleading, because these parameters assume an asymptotic behavior of the population given sufficient time and thus are

likely to overestimate the future growth of a population (Burgman et al. 1993). Unlike these studies, I introduced stochasticity into the model by varying vital rates over time and repeating the simulations 100 times. This probabilistic framework has the advantage of allowing assessment of various risks of population decline, rather than producing a point estimate based on a given set of input vital rates. Overall, estimates of projected population abundance were precise based on the magnitude of the confidence intervals.

The simulations also indicate that the only sustainable strategy when fishing at a constant rate of $F = 0.1$ is the exploitation of neonate and young-of-the-year sandbar sharks (stage 1), but harvesting of any other stages, in particular large juveniles, yields declining populations well before the end of the 20-year projections. Cortés (1998) found in a yield-per-recruit (YPR) analysis that only F values less than 0.1 could be applied to sandbar sharks older than age 15 to yield sustainable YPR values ranging from 5 to 35 kg/recruit. Similarly, Sminkey and Musick (1996) used life tables to determine that if F was applied starting at immature ages, the population would decline unless F was less than 0.1, based on a 30-year longevity scenario. While these two studies essentially concluded that only very low values of F are sustainable, results are not directly comparable with those of the present study, because of their use of deterministic life tables, and also because F values in those studies were applied starting at a certain age and including all age groups thereafter, not selected stages as in here.

The findings in the present study do not mean that present levels of fishing mortality should be shifted toward first-year sandbar sharks. They suggest that if a constant sustainable F value were to be applied, the least susceptible stage would be that consisting of newborn and young-of-the-year individuals, whereas harvesting of large juveniles should be avoided. However, it remains unclear how this would affect sandbar shark populations if present abundance has indeed been reduced by 60–80% with respect to that of the 1970s as suggested by trends in catch per unit of effort (Musick et al. 1993).

The simulations under the three alternative harvesting scenarios showed that the current quota would produce declining populations to different degrees. Assuming that the figures used to calculate removal rates are anywhere close to reality, removal of first-year (stage 1) and small juvenile (stage 2) sandbar sharks would produce
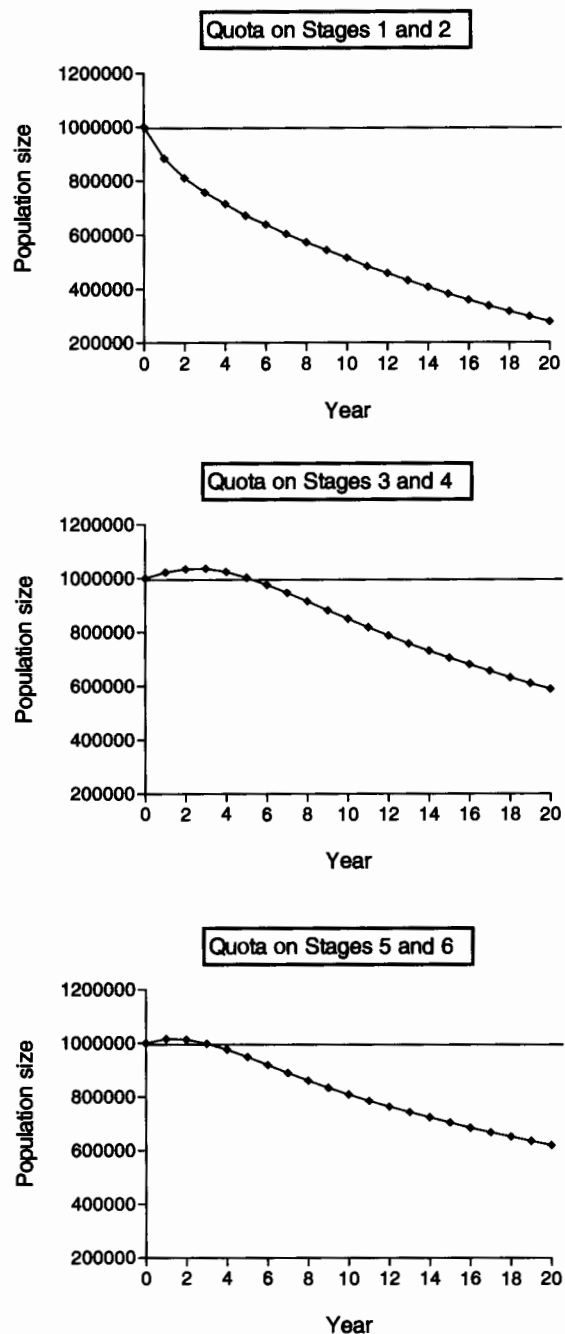
FIGURE 5.—Mean trajectories simulating the future abundance of a population of sandbar sharks in the northwest Atlantic over a 20-year period when subjecting stage 1 (neonate and young-of-the-year) and 2 (small juvenile), stage 3 (large juvenile) and 4 (subadult), and stage 5 (young adult) and 6 (large adult) individuals, respectively, to a removal rate equivalent to the current U.S. commercial quota. Each curve is the mean of 100 realizations, each of which started at Year 0 with a stable stage distribution of 1,000,000 females. Abundance at each subsequent time step was determined by randomly choosing birth and death rates from statistical distributions, but keeping the quota-based removal rate constant.

TABLE 3.—Intrinsic rates of population change for sandbar sharks in the northwest Atlantic.

Study	r (% per yr)
Hoff (1990)	1.8
Sminkey and Musick (1996)	−0.1 – 11.9
Au and Smith (1997)	2.1
Cortés (1998)	−1.9 – 0.3
This study	1.3

a precipitous decline. This result is not in conflict with the finding that harvesting of stage 1 at $F = 0.1$ results in slowly increasing populations and harvesting of stage 2 at $F = 0.1$ yields only moderately decreasing stocks. This is because the application of the current quota on these two stages represents a very high proportion of the stage abundance being removed each year: 62% for stage 1 and 20% for stage 2. The dusky shark *Carcharhinus obscurus* fishery in southwestern Australia is apparently an example of sustainable exploitation of age-0 individuals, which make up to 75% of the catch by number (Simpfendorfer 1999, this volume). The effect of this strategy on population abundance, however, should be tracked for at least the time it takes individuals to reach sexual maturity and reproduce and thus contribute additionally to the population. The advantage of this strategy lies in that it would allow immature and adult sharks to recover.

Harvesting larger but still immature sandbar sharks (stages 3 and 4) at the present levels is also a risky strategy. While subadults may be harvested at $F = 0.1$ and yield only slightly decreasing populations, large juveniles are very susceptible, indicating that the quota should be reduced. Branstetter (1996) reported that about 50% of the landings in North Carolina are composed of immature individuals generally caught in nearshore waters. Although this size segregation may not be the same throughout its range, decreased fishing pressure in these areas through area closures may have a positive impact on sandbar shark population size, especially considering that these areas are also utilized at certain times by pregnant females (Branstetter 1996).

Harvesting of adults, both young and older (stages 5 and 6), at the present levels is not a satisfactory alternative either. When exploited at $F = 0.1$, young adults were found to be the second-most vulnerable stage, but even removal of older adults at $F = 0.1$ resulted in population declines. Removal of mostly adult sandbar sharks is prob-

ably the strategy that more closely resembles the current situation in the U.S. Atlantic shark fishery. While this strategy would allow protection of immature stages, a quota reduction is required according to the present study, probably because of recruitment overfishing (Cortés 1998).

There are several potential sources of bias that may have affected my analysis. First, I introduced the assumption that the initial stage distribution was stable, based on life table results by Cortés (1998) indicating an almost stationary population. Because the purpose of the simulations was to project the population forward in time given an initial state, not necessarily representing the present status of the population, the major conclusions of my analysis are still valid. Admittedly, sandbar sharks have been heavily exploited for at least one decade, and it is thus likely that the present age and stage distributions have shifted from equilibrium. However, it is reasonable to assume that the stage distribution was stable before exploitation, especially because there is no other demographic information on population size and structure upon which to base any other initial status.

Second, my model did not incorporate any density-dependent compensatory mechanisms or migratory rates into or out of the population. I chose not to include these aspects of population dynamics because of the limited information on any of those putative mechanisms for the sandbar shark. Sminkey and Musick (1995) found evidence, however, of small compensatory density-dependent changes in growth rate in juveniles after heavy exploitation, although age at maturity remained the same as before exploitation. There is presently no evidence of compensatory changes in reproductive parameters in the sandbar shark. And while a better picture of the migratory routes and habits of this species is emerging, migration rates are still unknown.

Compensatory changes in survival rates of pups or young animals are another potential mechanism of population regulation. Indeed, they have been found or proposed to explain population regulation in other long-lived marine and terrestrial vertebrate animals, including northern fur seals *Callorhinus ursinus* (Smith and Polacheck 1981), grey seals *Halichoerus grypus* (Harwood 1978), northwest Atlantic harp seals *Pagophilus groenlandicus* (Lett et al. 1981), and African elephants *Loxodonta africana* (Fowler and Smith 1973) to cite a few examples.

In sharks, Walker (1992) proposed density-dependent prerecruit natural mortality as a regulatory mechanism for the gummy shark *Mustelus antarcticus* off southern Australia. Cortés and Parsons (1996) also conjectured that increased offspring size of bonnetheads *Sphyrna tiburo* could enhance the probability of survival of young-of-the-year individuals and thus act as a regulatory mechanism. While a similar mechanism may be operating to regulate population size in sandbar sharks, the high values of survivorship for young-of-the-year and juvenile individuals used in my simulations—starting at 74% annual survival—leave little room for compensation. In all, potential density-dependent compensatory effects are likely to be small within the time frame of the analysis compared with the impact of the harvest levels tested.

Third, my choice of stages was somewhat arbitrary despite being based on the biology of this species and corresponding well with the groupings identified by Musick et al. (1993). The stages considered in the model were based both on length and age (stage duration). All transformations between length and age and vice versa were based on the von Bertalanffy growth model and were biased given the inherent variability in length at age and age at length. More detailed models could be constructed that incorporated a probability distribution of ages at length and, conversely, of lengths at age. This, however, was beyond the scope of the present simulation exercise.

This study did not exhaustively explore all possible management strategies and harvesting levels that would result in sustainable stocks. For example, a combination of moderate pup harvest and adult harvest or of male harvest alone under a quota or a constant proportion of the population may be sustainable strategies. Clearly, more work is needed to identify the management strategies that can result in stable and resilient sandbar shark stocks. However, results indicate that the present quota is too high and definitely not sustainable if the value of initial population size reasonably represents virgin stock biomass levels for sandbar sharks.

Studies with other vertebrates have found results similar to those in the present study. For example, Crouse et al. (1987) found that the most vulnerable stages in loggerhead sea turtles *Caretta caretta* were juveniles and subadults, especially large juveniles, and not eggs and hatchlings as assumed by management practices.

In conclusion, this work suggests that large juveniles, 1–1.5 m in length, may be the most vulnerable stage in the life cycle of sandbar sharks and that age-0 individuals may possibly be harvestable at low levels of exploitation after the stock recovers. More information needs to be collected on the present spatiotemporal distribution of the various stages by gender if future management of this resource is to target specific life stages.
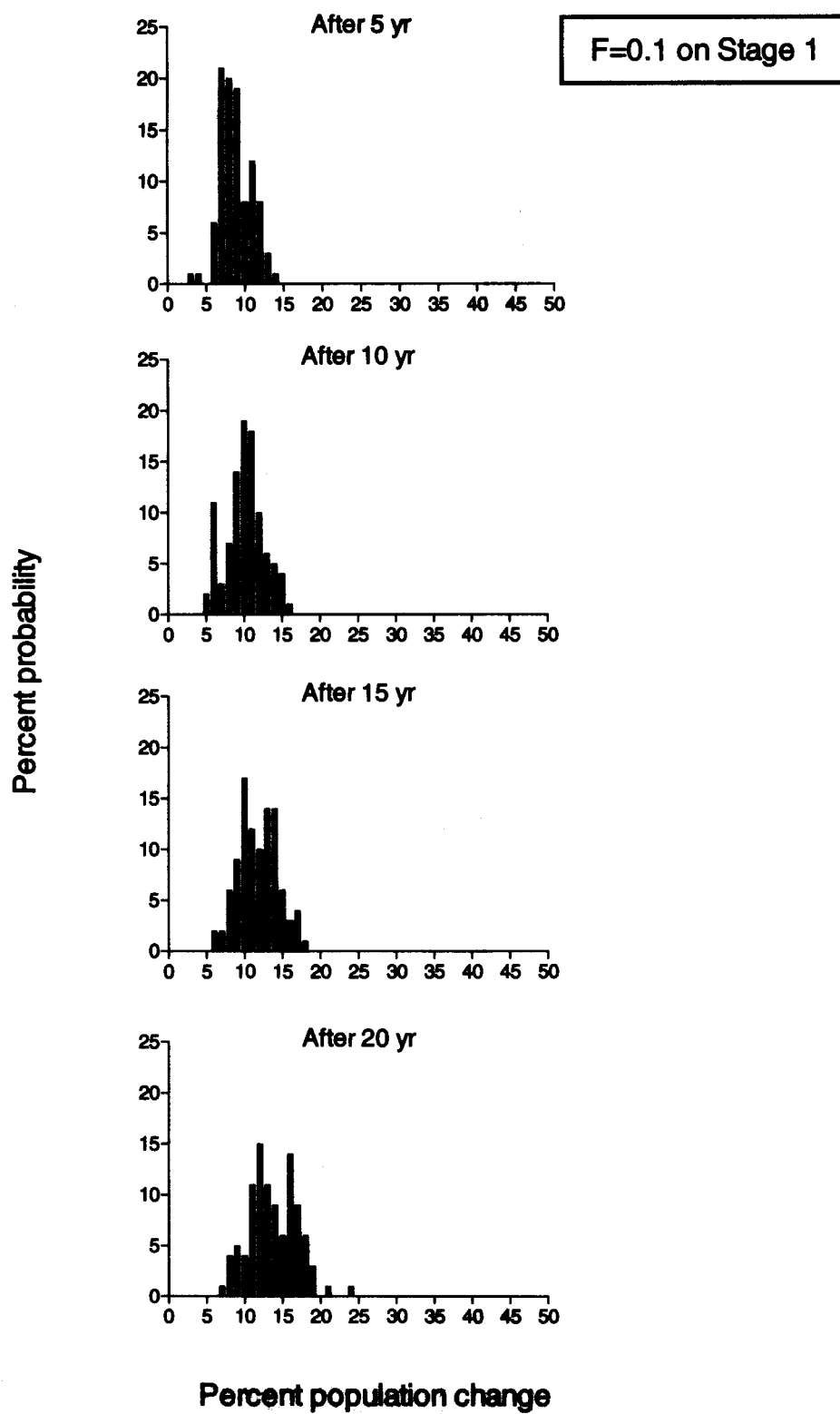
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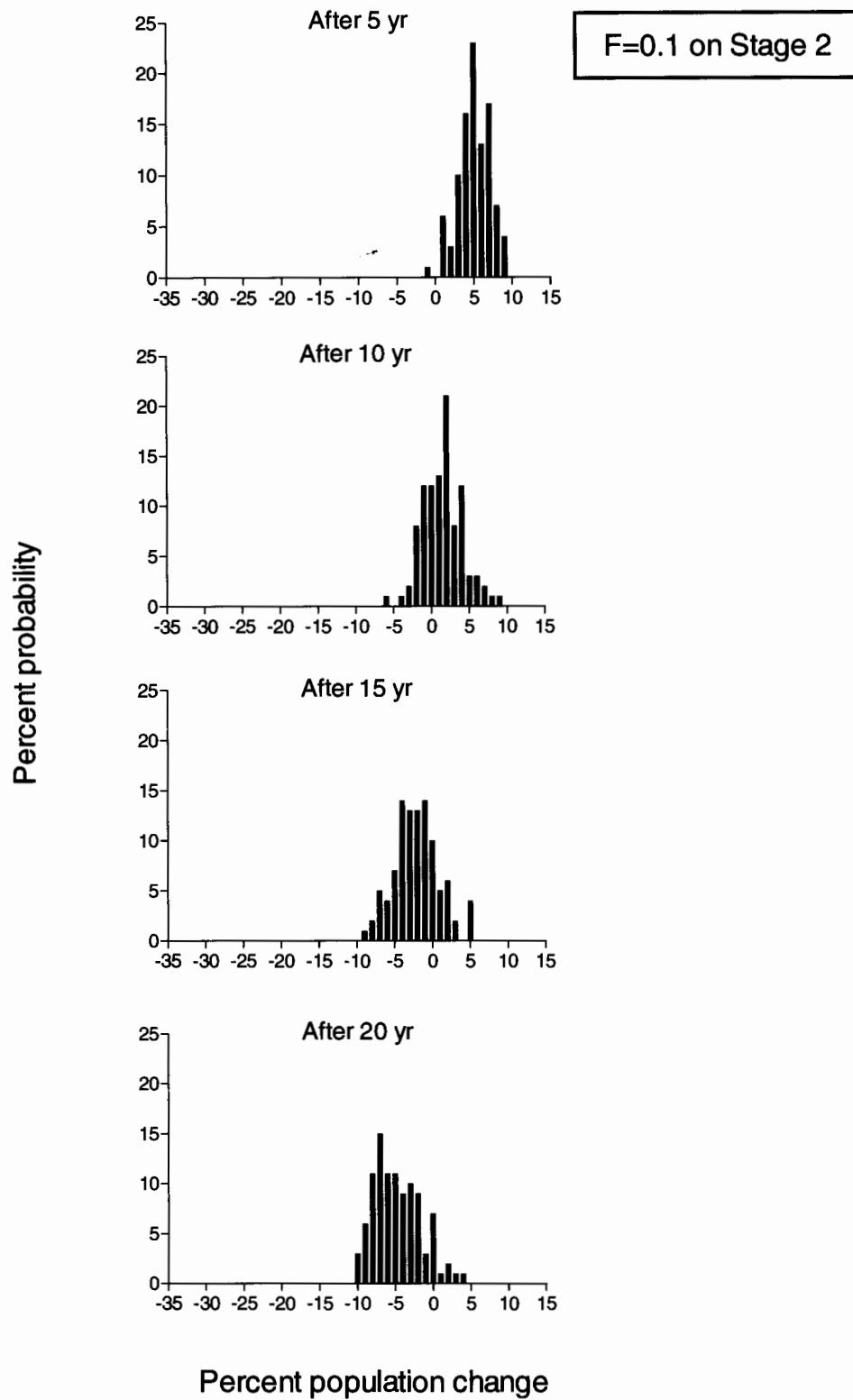FDEP (Florida Department of Environmental Protection). 1996. Marine fisheries information,

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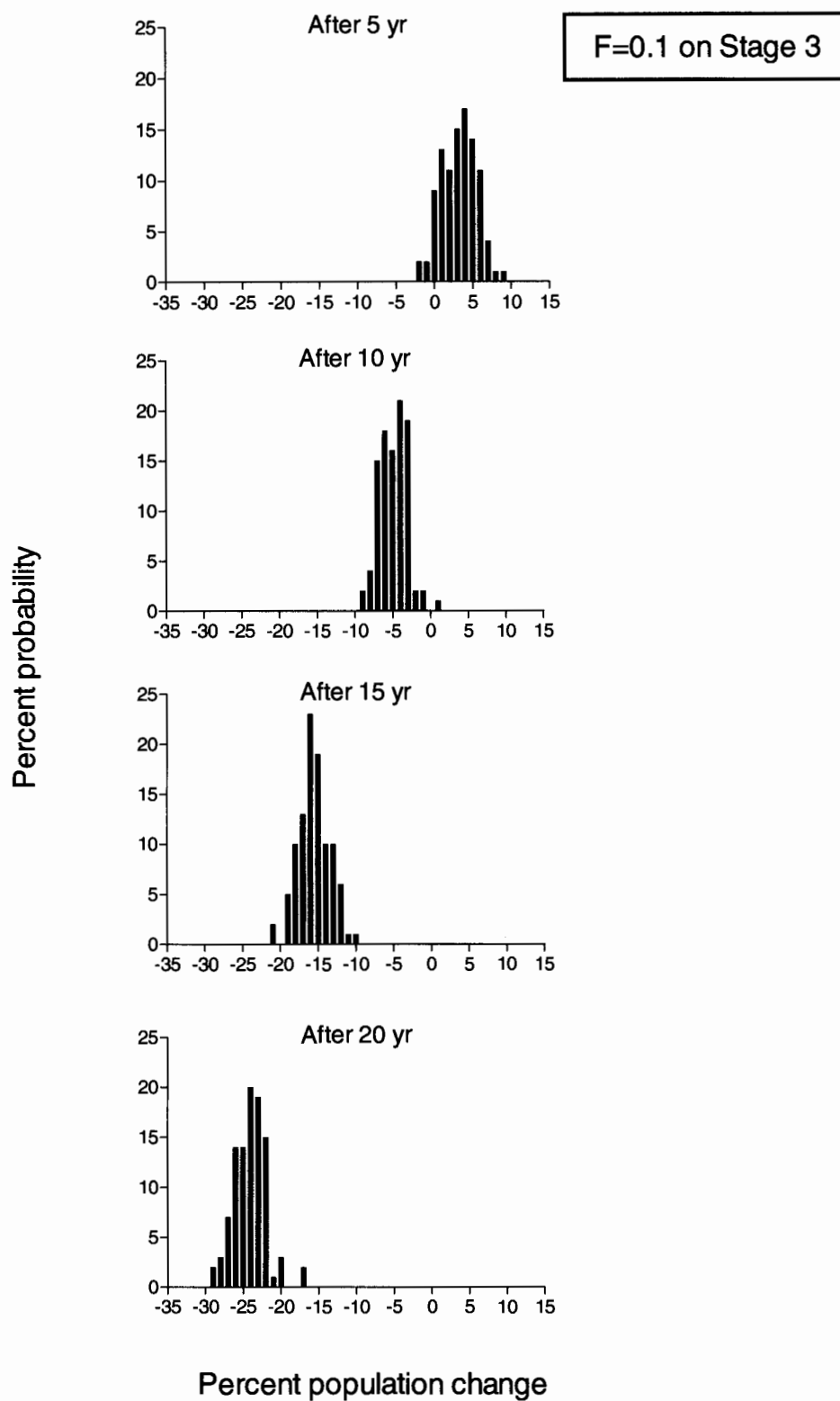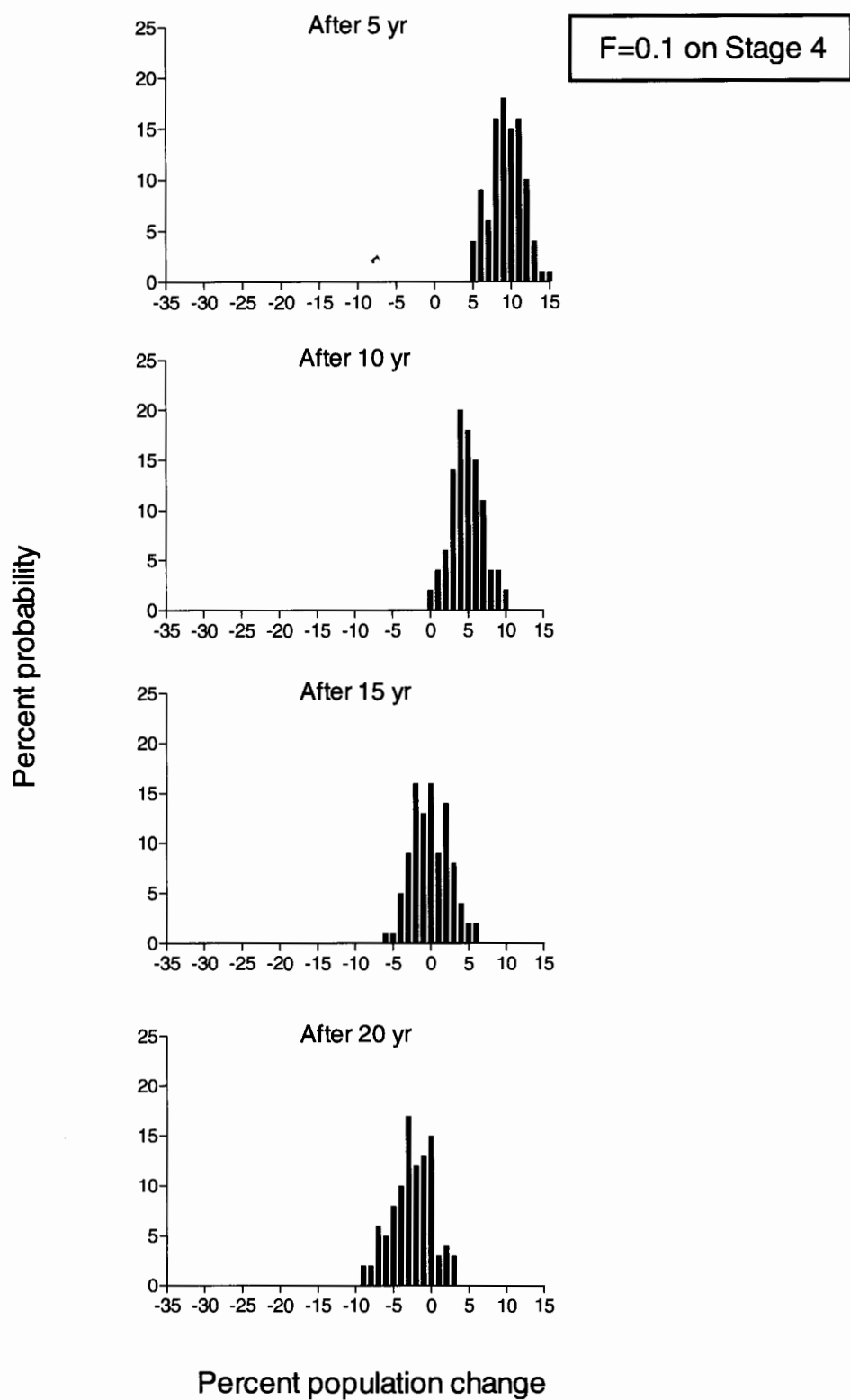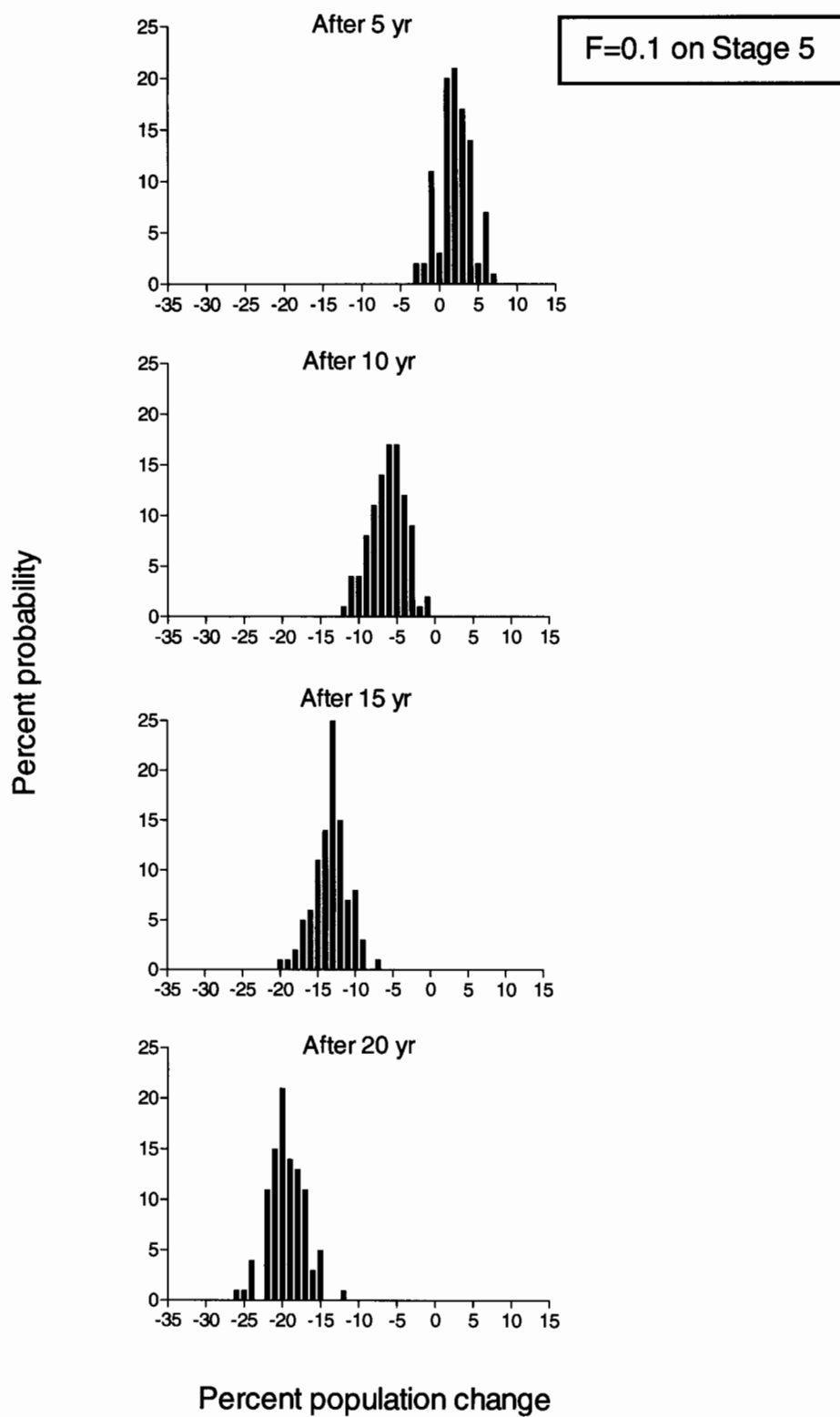
Appendix
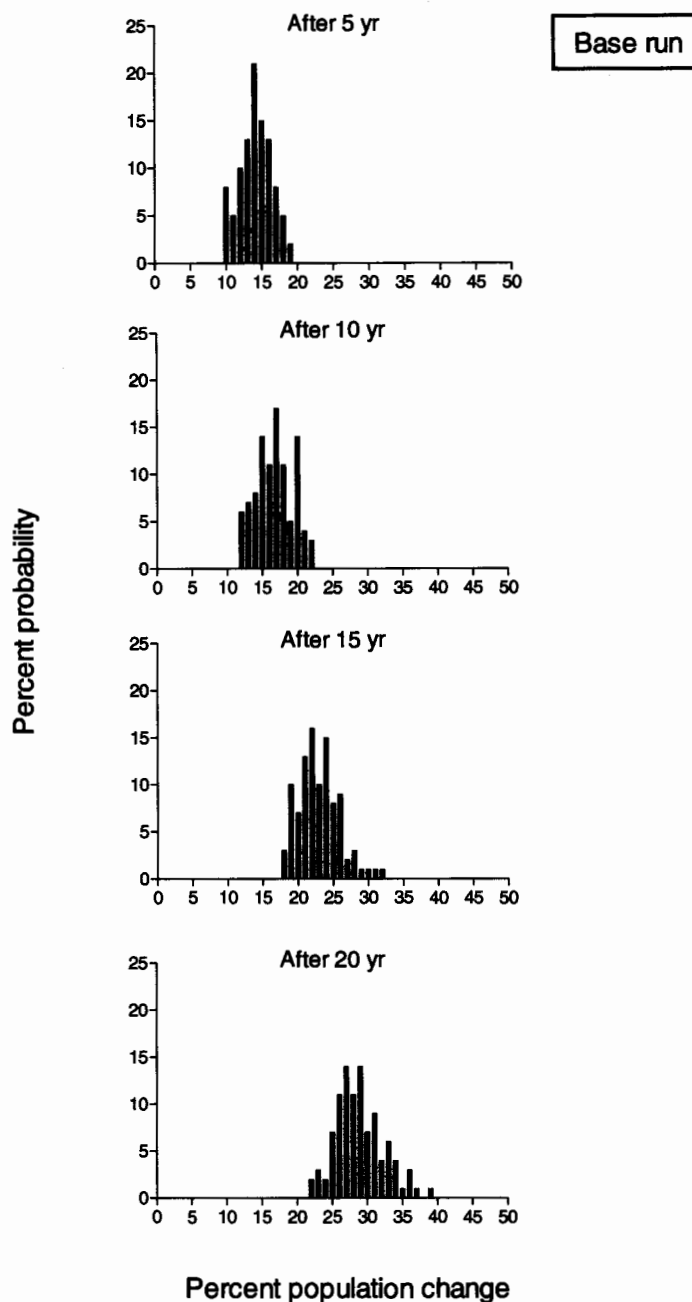
APPENDIX FIGURE 1.—Sets of histograms of the percent probability of various levels of population change relative to the initial population size at four selected time steps. The runs simulate an unexploited population (base run) of sandbar sharks and a population selectively subjected to a removal rate of $F = 0.1$ on stage 1 (neonate and young-of-the-year), stage 2 (small juvenile), stage 3 (large juvenile), stage 4 (subadult), stage 5 (young adult), or stage 6 (large adult) individuals, respectively.
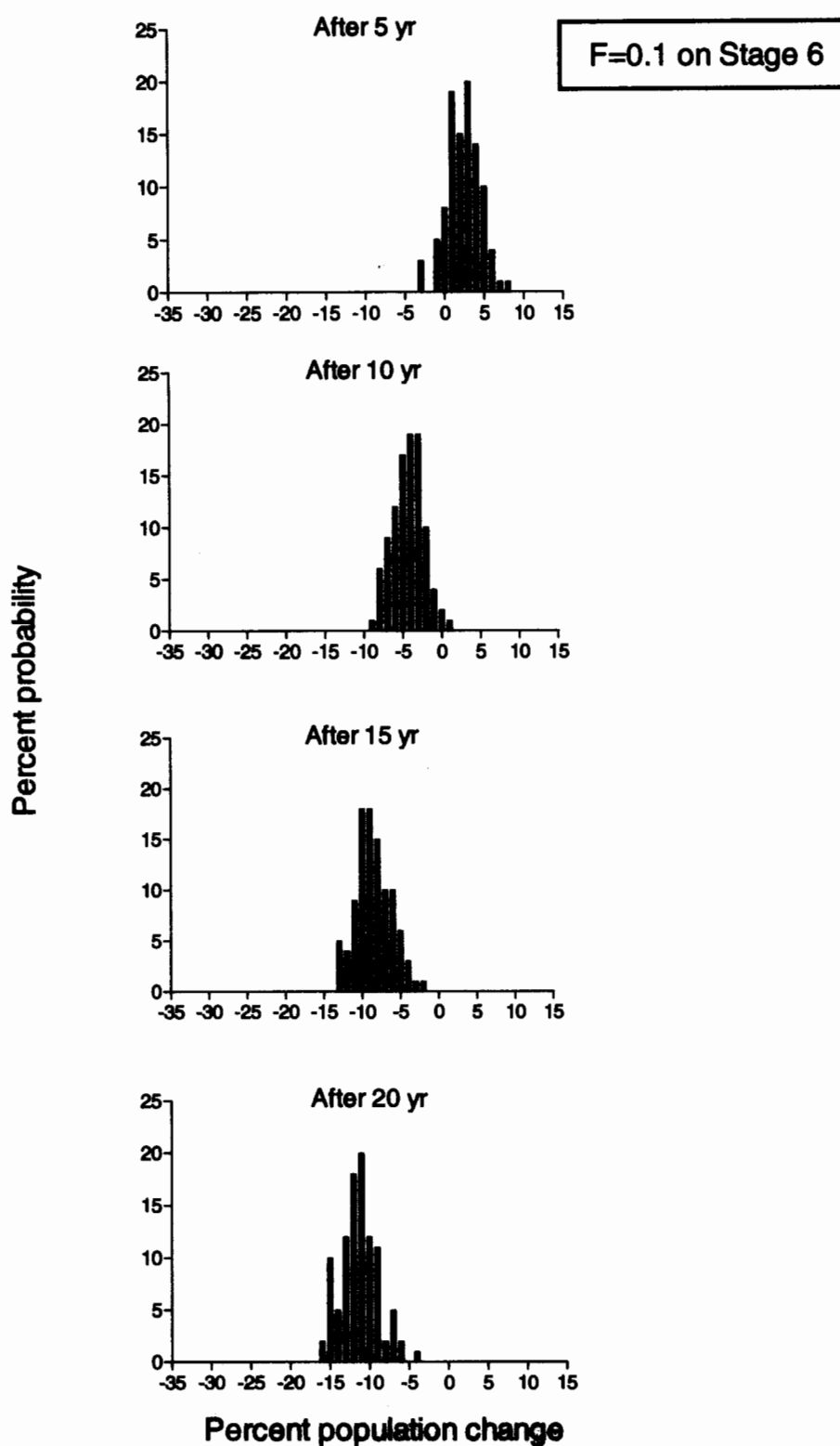
After 5 yr

F=0.1 on Stage 1

After 10 yr

Percent probability

After 15 yr

After 20 yr

Percent population change

F=0.1 on Stage 2

After 5 yr

After 10 yr

After 15 yr

After 20 yr

Percent probability

Percent population change

Percent population change

F=0.1 on Stage 4

After 5 yr

After 10 yr

After 15 yr

After 20 yr

Percent probability

Percent population change

After 5 yr

F=0.1 on Stage 5

After 10 yr

Percent probability

After 15 yr

After 20 yr

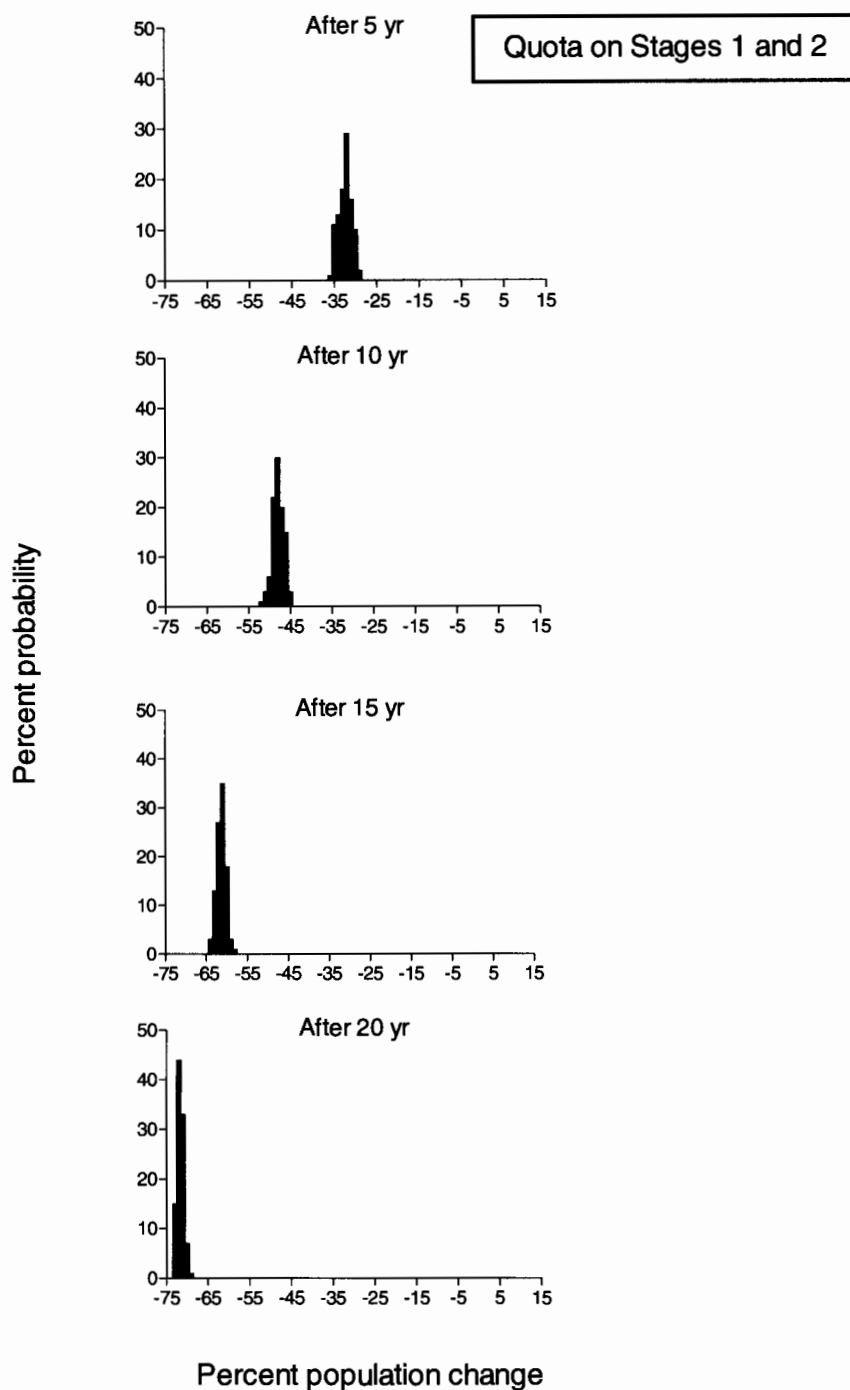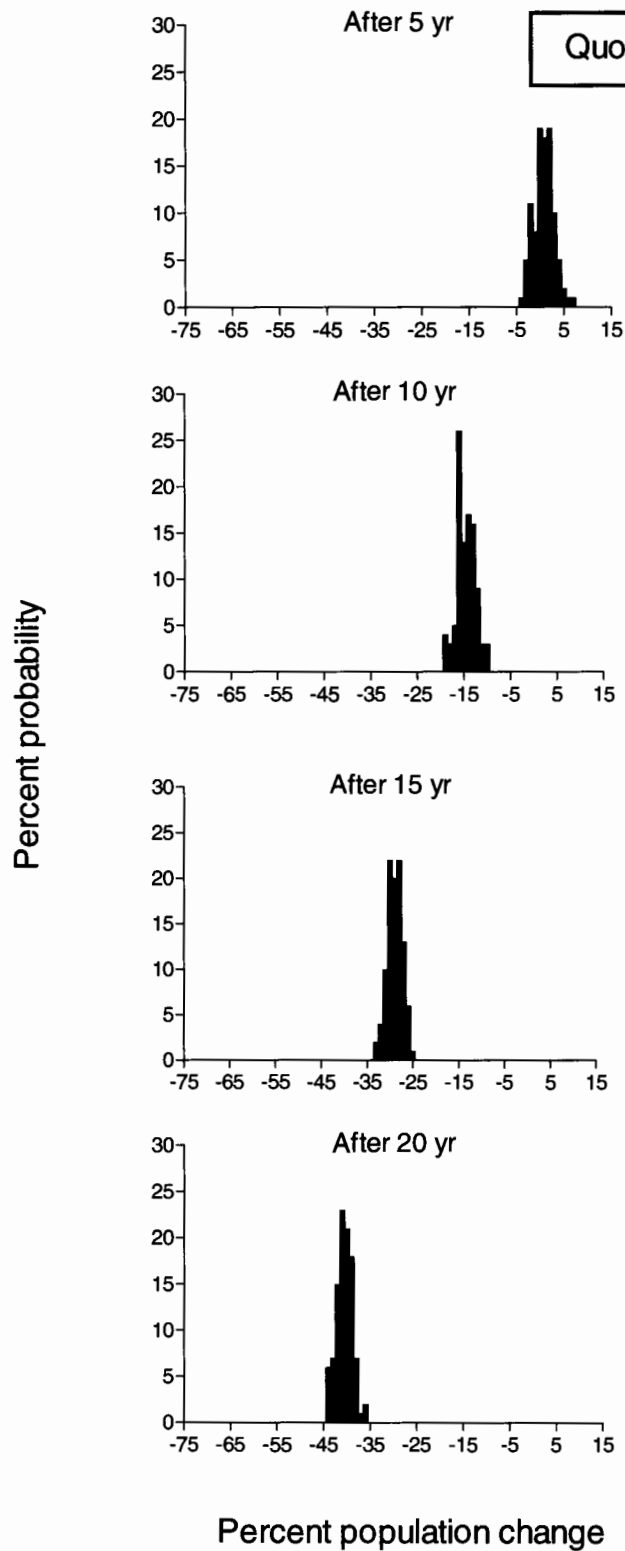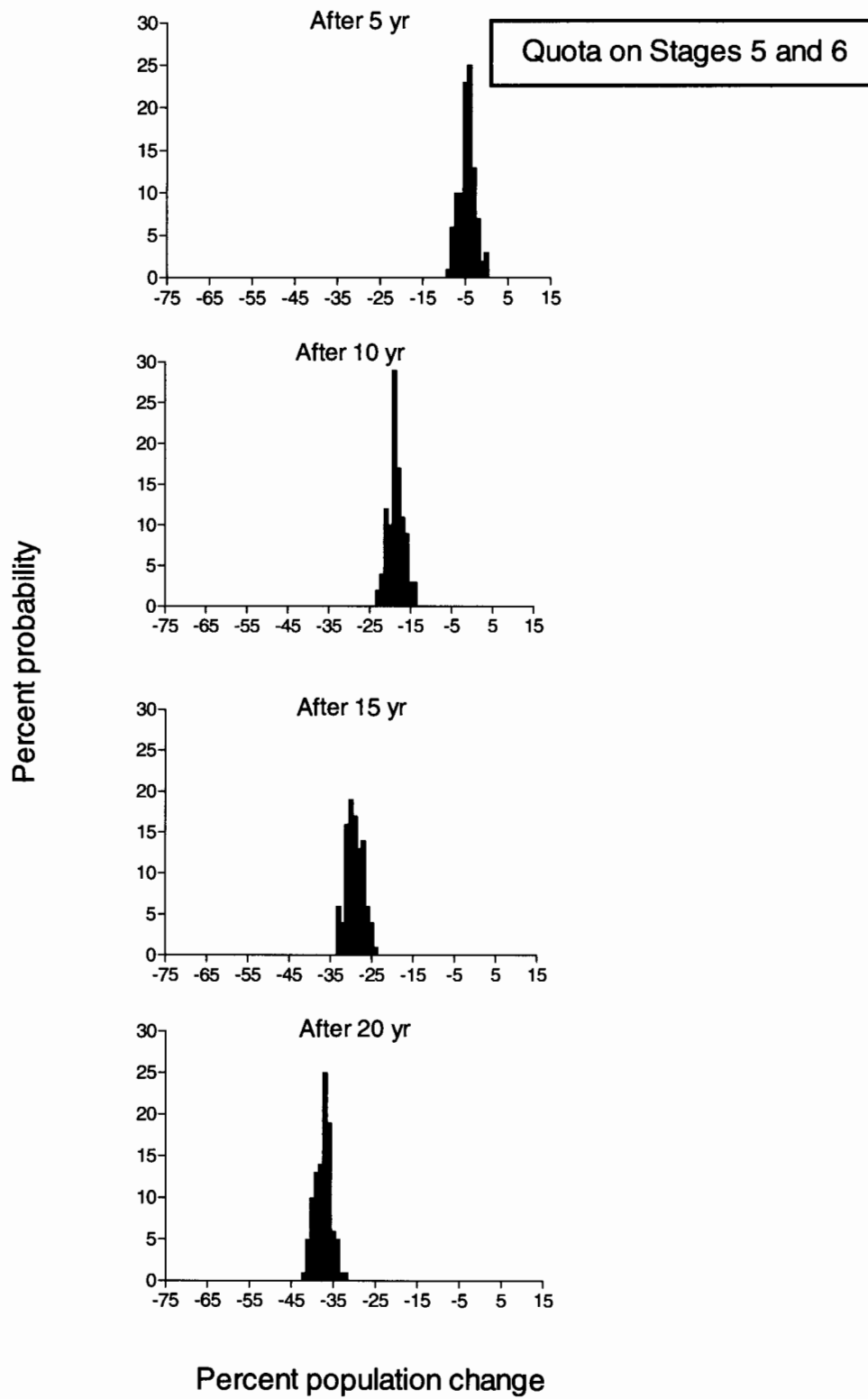Percent population change

F=0.1 on Stage 6

APPENDIX FIGURE 2.—Sets of histograms of the percent probability of various levels of population change relative to the initial population size at four selected time steps. The runs simulate a population of sandbar sharks selectively subjected to a removal rate equivalent to the current U.S. commercial quota on stages 1 (neonate and young-of-the-year) and 2 (small juvenile), stages 3 (large juvenile) and 4 (subadult), or stages 5 (young adult) and 6 (large adult) individuals, respectively.

Quota on Stages 3 and 4

After 5 yr

After 10 yr

After 15 yr

After 20 yr

Percent probability

Percent population change

Percent population change

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Edited by

John A. Musick
Virginia Institute of Marine Science
College of William and Mary

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